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BIOLOGICAL BULLETIN

SOME ANOMALIES IN THE GESTATION OF THE ALBINO RAT (*MUS NORVEGICUS ALBINUS*).

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In the course of a series of inbreeding experiments with the albino rat which have been in progress for several years, records have been made of the births of over 700 litters containing some 5,000 individuals. These records show a number of striking irregularities in gestation which are deemed worthy of note, since at the present time the albino rat is extensively used as a laboratory mammal in many of the large institutions of the country.

As the data given in this paper form part of the permanent records on file at The Wistar Institute, it has seemed advisable to refer to individual rats by the numbers that will identify them on the record cards, instead of employing some conventional lettering. The scheme for designating the rats, which is outlined below, has been found very satisfactory for keeping track of a large number of individuals, since it tells at once the pedigree of any particular animal. In the scheme of marking used the serial letter, *A* or *B*, indicates that the individual was a descendant of one or of the other of the two females, *A* and *B*, with which the experiments were started in the spring of 1909. The serial letter is preceded in all cases by a number which shows the generation to which the rat belonged. An index number, following the serial letter, indicates in which of its mother's litters the animal was born: if no index number is present the rat was a member of its mother's first litter. The subscript following the serial letter is the number that serves to distinguish each particular rat from the other individuals belonging to the same generation and litter group. An illustration of this method of designating the

rats will, perhaps, make the scheme somewhat clearer. $6B_{57}^2$ for example, denotes a female belonging to the sixth generation of rats that descended from female *B*. She was a member of the second litter borne by her mother, and her individual number in the series of rats belonging to the second litters of the sixth generation was 57.

It is part of the daily routine work in the rat colony to examine the cages containing breeding animals and to record the births of litters. The birth of a litter is ascribed to the day on which the litter is discovered, unless it is evident from the appearance of the young rats that their birth had been overlooked at a previous visit. In the latter case an approximate date is assigned for the birth of the litter, and on the record cards this date is followed by an interrogation mark. As the rat colony is usually visited in the morning it is very probable that, in the majority of cases, a litter is discovered shortly after its birth, since observations made at various times indicate that in the rat parturition occurs most frequently in the morning, although it may take place at any time during the day. All of the dates of the births of litters given in the present paper are correct within a few hours, since no cases have been included in which a litter was obviously more than a day old when discovered.

As a rule the male is removed from the breeding cage just before, or immediately after, the birth of a litter in order to guard against the possibility of his destroying the young rats. This is seemingly a needless precaution, since infanticide is comparatively rare in albino rats, although it is very common among brown rats kept in captivity according to the observations of Miller ('11). When young albino rats are destroyed it is done, as a general thing, by the female, either because her nest is disturbed during parturition or because she is not in a physical condition to suckle her offspring and is annoyed by their attempts to obtain food. In only one case, as yet, have I found a male eating the young, and in this instance the female was equally as guilty as her mate.

The anomalies in gestation that are noted in the present paper are of three kinds: (1) Prolongation of the period of gestation; (2) cases of superfecundation; (3) cases of superfoetation.

I. PROLONGATION OF THE PERIOD OF GESTATION.

According to a series of unpublished records kindly furnished me by Dr. J. M. Stotsenburg, of The Wistar Institute, the time between the copulation of a non-lactating albino rat and the birth of her litter varies from 21 days and 15 hours to 22 days and 16 hours. The normal period of gestation for the albino rat, therefore, can roughly be estimated at from 21 to 23 days. In the brown rat kept in captivity the period of gestation seems to be somewhat longer than in the albino rat, as Miller found that it varies from $23\frac{1}{2}$ days to $25\frac{1}{2}$ days in different cases.

Daniel's ('10) investigations show that in the mouse the period of gestation, which is normally 20 days, is considerably prolonged if the female is suckling young. From data obtained in ten cases he formulates the following law: "The period of gestation, in lactating mothers, varies directly with the number of young suckled." In the course of my experiments records have been made of the births of 31 litters borne by lactating albino rats. These records, as shown in the three following tables, indicate that the length of the period of gestation is affected by the number of young suckled and by other factors as well.

Table I. shows the length of the period of gestation when lactating females were suckling five or less young and carrying five or less young.

TABLE I.

Number of Female.	Date of Birth, First Litter.	No. Young Suckled.	Date of Birth, Second Litter.	No. Young Born.	Gestation Period, Days.
5A ₂	July 14	3	Aug. 8	5	21
2A ₁ ²	Aug. 26	4	Sept. 9	5	21
5A ₂₇	Dec. 28	5	Jan. 18	4	21
7A ₇₆	June 21	5	July 13	5	22
4A ₁₅	May 23	4	June 6	3	23
8A ₈	Aug. 14	4	Sept. 9	5	23
5A ₁₆	Nov. 15	5	Dec. 8	3	23
4B ₂₄	June 14	5	July 7	5	23

In each of the eight cases cited above the period of gestation can be considered as normal since it did not exceed 23 days. It appears, therefore, that the period of gestation in lactating albino rats is not extended if the number of young suckled and the number of young in the second litter does not exceed five in either case.

In Table II. are given the data for cases in which the number of young suckled was five or less while the number of young in the second litter exceeded five.

TABLE II.

Number of Female.	Date of Birth, First Litter.	No. Young Suckled.	Date of Birth, Second Litter.	No. Young Born.	Gestation Period, Days.
2B ₁ ²	June 8	3	June 29	7	21
1B ₁	Jan. 15	3	Feb. 5	8	21
6A ₈₈	April 24	5	May 17	8	23
4B ₁₃	June 2	4	June 26	6	24
4A ₂₉	Dec. 20	4	Jan. 14	7	25
5A ₂₆	Nov. 20	4	Dec. 14	9	25
8B ₈₂	Aug. 20	3	Sept. 15	13	26
5B ₄ ²	Aug. 30	3	Sept. 26	8	27
4B ₃₃	Aug. 3	4	Aug. 30	8	27
3A ₃	Jan. 15	4	Feb. 12	7	28
5B ₃ ²	Sept. 11	5	Oct. 10	12	29

In eight of the eleven cases shown in Table II. the period of gestation was prolonged from one to six days. In the three remaining cases the gestation period was normal since it did not exceed 23 days. These results indicate that, as a rule, the period of gestation is prolonged when a lactating female, suckling a small number of young, is carrying a litter containing six or more embryos.

Table III. shows the length of the period of gestation in lactating females suckling more than five young.

TABLE III.

Number of Female.	Date of Birth, First Litter.	No. Young Suckled.	Date of Birth, Second Litter.	No. Young Born.	Gestation Period, Days.
5A ₁₈	Dec. 8	7	Jan. 2	6	25
5A ₄	Nov. 25	7	Dec. 20	8	25
7A ₇₆	Sept. 11	6	Oct. 7	3	26
5B ₁	July 4	6	July 30	9	26
4B ₄₀	July 13	6	Aug. 8	10	26
8A ₇₆	Sept. 16	6	Oct. 13	5	27
8A ₉	Sept. 13	7	Oct. 11	5	28
5B ₃₂	Oct. 5	8	Nov. 5	8	30
8B ₂₇	June 1	10	July 1	8	30
8A ₆₁	Sept. 13	9	Oct. 14	4	31
4B ₆₁	July 26	11	Aug. 28	12	33
6B ₃ ² ₇	May 24	9	June 27	12	34

Since in the twelve cases recorded in Table III. the period of gestation ranged from a minimum of 25 days to a maximum of

34 days it is evident that the suckling of more than five young prolongs the period of gestation in the albino rat. The length of the gestation period is not, as a rule, directly proportional to the number of young suckled. For, assuming 22 days to be the average length of the gestation period, only three of the twelve cases fulfill the conditions of Daniel's law. In the majority of cases shown in Table III. the length of the period of gestation seems to have been little affected by the number of young in the second litter. For instance, female 7A₇₆, with six young in her first litter, had a gestation period of 26 days before the birth of a second litter containing three individuals; on the other hand, females 5B₁ and 4B₄₀, each suckling six young, also had gestation periods of 26 days when there were nine and ten young respectively in their second litters. In some few cases, however, the gestation period seems to be further prolonged if a lactating female is carrying a very large litter. This is indicated by the fact that the two longest gestation periods yet recorded, 33 and 34 days, were found only when the second litter contained an unusually large number of individuals.

The data given in the above tables show that the period of gestation in lactating albino rats varies from a minimum of 21 days to a maximum of 34 days. The length of the gestation period seems to depend, primarily, on factors that affect the nutritive conditions of the embryos, but it is also influenced, to some extent, by the individual peculiarities of the females. Lactating females may have different periods of gestation when the number of young in each of their litters is the same, as is shown in the case of females 3A₃ and 4A₂₉. Each of these females had four young in her first litter and seven young in her second litter, yet the former had a gestation period of 28 days before the birth of her second litter, while in the latter female the gestation period was only 25 days.

A comparison of the data given in Table II. with that shown in Table III. indicates that in different lactating females the period of gestation is not as extended when five or less young are suckled as when this number is exceeded. This rule seems to apply equally well also to the different litters borne by the same female. Female 7A₇₆, when suckling five young, had a

gestation period of 22 days before the birth of a second litter containing five young; when suckling a litter of six the period of gestation was prolonged to 26 days although there were but three young in the second litter. Why the suckling of six instead of five young should invariably prolong the period of gestation is not at all clear. Records of some 800 litters of albino rats show that the average number of young in a litter is six. Seemingly, therefore, the length of the gestation period is prolonged when the number of young suckled equals or exceeds the number that represents the average size of the litter in the species.

Female $6B_{87}^2$ had a gestation period of 34 days, the longest period so far observed. This case is rather an interesting one. The nine young born on May 24, 1912, were suckled until June 20, when it was noticed that the female was pregnant. As the young rats were well developed and able to care for themselves they were removed from the cage, although, under ordinary conditions, a litter is allowed to remain with its mother for a month. The female was watched closely, and parturition was found to take place on the morning of June 27. There was thus a period of one week after the removal of the first litter before the second litter was born, although the normal period of gestation had been passed before the first litter was taken away. Had the young rats in the second litter reached the proper stage of maturity for birth when the first litter was removed it is very probable that they would have been born immediately. In this instance, therefore, lactation did not merely delay parturition but it must have retarded the development of the embryos.

The young rats in the second litter were examined shortly after their birth. They were normal in appearance, but they were very small, weighing not more than 4 gm. each. According to Donaldson ('06), the weight of the albino rat at birth varies from 4.2 gm. to 6.5 gm. As the size of the newborn rat depends to a very considerable extent on the number of individuals in the litter, no significance can be attached to the fact that in this very large litter the rats at birth weighed less than 4.2 gm. each. As it was not considered advisable to allow the female to suckle so many young, six of them were killed at once. The others developed normally, and opened their eyes at the usual

time, *i. e.*, when 15 days old. The prolonged period of gestation did not make these young rats more precocious in any way as far as could be determined.

In the rat, as in the mouse according to the observations of Sobotta ('95) and of Long and Mark ('11), ovulation followed by copulation must normally take place within a few hours after parturition, since in all of the cases recorded in the above tables the male was removed shortly after the birth of the litter and the female with her young occupied a cage inaccessible to the entrance of other rats. In none of the cases cited in Table I. could lactation have delayed ovulation, since in each instance the period of gestation was of normal length. The manner in which the experiments were conducted seems to preclude the possibility that the prolonged periods of gestation found in many cases were due to a delay in ovulation caused by lactation, since presumably mammalian spermatozoa are not functionally active for more than two or three days after insemination, although, according to Schultze ('66), they can live in the uterus for as much as six days. It seems probable, therefore, that lactation prolongs the period of gestation by influencing the nutritive conditions of the developing embryos. In the lactating albino rat the physiological conditions affecting nutrition seem to be so adjusted that the suckling of a small number of young does not interfere at all with the development of a second litter which also contains a small number of young. When the number of rats suckled equals or exceeds the number that represents the average size of the litter in the species, then lactation appears to lessen the amount of nourishment that the developing embryos receive. It seems to be more essential for the welfare of the species that the suckling young should be well nourished than that the foetal young should develop at the normal rate. When a pregnant female is suckling a large number of young, the embryos receive less nourishment than is usually given by a non-lactating mother and consequently they develop more slowly. In cases of this kind the period of gestation is prolonged until the embryos have reached the proper stage of maturity for birth. When a female is suckling a small number of young and carrying a large litter, there is apparently no readjustment of the nutritive conditions

so that each foetus will get the nourishment that will enable it to develop in the usual time. The development of ten or of a dozen embryos on nourishment normally used by six means, necessarily, that the embryos will develop more slowly and therefore that the period of gestation will be prolonged.

The causes that determine whether the period of gestation in non-lactating albino rats shall be 21 days or 23 days are as yet unknown. Presumably the size of the litter is a determining factor in these cases as well as in those in which a female is already suckling young. The age and physical condition of the female are also factors that are probably of importance in this regard. A very young female or one in poor condition would not be able to nourish her foetal young as well as would a more mature female in good condition, consequently the period of gestation would tend to be longer in the former case than in the latter.

The extension of the period of gestation in the albino rat from 21 days to 34 days is not a remarkable phenomenon, since the early observations of Tessier, quoted in detail by Collins ('86), show that the duration of the gestation period in various mammals is subject to considerable variation.

The data furnished by Collins and Daniels give the extremes of gestation periods shown in Table IV.

TABLE IV.

Mammal.	No. Cases Observed.	Shortest Period of Gestation, Days.	Longest Period of Gestation, Days.	Difference Between the Extremes, Days.
Cows.....	575	240	321	81
Mares.....	447	287	419	132
Sheep.....	912	145	156	11
Swine.....	25	109	133	24
Rabbits.....	161	27	35	8
Mice.....	10	20	30	10

In none of these cases is the duration of the gestation period relatively as long as in some of the cases recorded in Table III., where the gestation period for the albino rat is shown to have been extended more than one half of the minimum normal period. The relatively greater length of the gestation period in the rat may not, however, be of any significance, since it is very probable that the periods of gestation given in Table IV. are not the longest

that have been observed in the various mammals mentioned, although I have not been able to find any records that exceed them.

2. CASES OF SUPERFECUNDATION.

As there is much confusion in literature regarding the use of the words superfecundation and superfœtation, it seems advisable to define these terms as they are employed in this paper. Superfecundation is used in cases where two or more ova belonging to the *same* period of ovulation were fertilized by successive matings. Superfœtation, on the other hand, is applied to cases in which ovulation, followed by copulation, occurred during pregnancy and led to the simultaneous development in the uterus of two sets of ova belonging to *different* periods of ovulation.

Although no observations have been recorded regarding the time required for parturition by the rat it is generally assumed that all members of a given litter are born within five or six hours, as is the case in the mouse according to the investigations of Long and Mark and of Daniels ('12). While this rule doubtless holds good in the great majority of cases there are occasional exceptions, as is shown by the following instance.

Female 8B₆ gave birth to a litter on April 8, 1912. It became necessary to move the mother and young the day after the litter was born. Six young rats were transferred to the new nest and all of them were apparently of about the same size and weight. Three days later the new nest was examined to see if the transference had caused the female to destroy her offspring. This time eight individuals were found in the litter; two of them were decidedly smaller than the rest and they had the appearance of having been born but a very short time. In this instance there was an interval of at least two days between the birth of the first six members of the litter and of the last two.

On examining litters of albino rats that are from six to fourteen days old one occasionally finds that one or more of the young rats are decidedly smaller and more immature than the others. Such small individuals have been considered by many investigators as runts, and their size has been attributed to the fact that, being constitutionally weaker, they were unable to obtain

as much nourishment as the other members of the litter and so had not grown as rapidly. The litter of 8B₅, described above, shows that in some cases the very great difference in the size of the various individuals in a young litter is not due to constitutional weakness on the part of the smaller individuals, but to the fact that the smaller rats were born two or three days after the larger ones.

In the course of my experiments I have found a number of litters, about two weeks old, in which one or more of the individuals were much smaller than the rest. Two instances will serve as examples of such cases. Female 4B₃₉ gave birth to a litter on October 27, 1911. When the litter was fourteen days old it was examined and found to contain twelve individuals. Ten of the young rats were in a similar condition of development; they weighed from 13.7 gm. to 14.4 gm. each; they were well covered with hair; and their eyes were beginning to open. The other two members of the litter appeared normal in every way; but their eyes were closed; they had comparatively little hair; and they weighed only 9.1 gm. and 9.3 gm. respectively. Judging from their appearance these small individuals were not more than ten days old.

A litter belonging to female 5B₁₉ was inspected thirteen days after its birth. Nine of the ten young were in approximately the same stage of development, and they weighed from 16.2 gm. to 17.1 gm. each. The tenth individual seemed normal and well nourished, but it weighed only 10.8 gm. and appeared more immature in every way than did the other members of the litter.

The small individuals in both of these litters were earmarked in order to make their identity certain, and they were allowed to grow up. At the end of two months there was no perceptible difference, either in size or in general behavior, between these individuals and the other members of the litter. The relatively small size of these rats when they were two weeks old did not mean, therefore, that they were constitutionally weaker than their fellows but that they were born later.

In litters of albino rats, especially if the litter is very large, it is not uncommon to find individuals that are less vigorous than the other members and that are stunted in their growth.

An instance recently came under my observation in which a male rat in a litter about three months old weighed only 60 gm., while his brothers and sisters all weighed from 130 gm. to 190 gm. each. This small individual was unquestionably a runt, and he was far less vigorous and active than the other rats in the litter. Runts that are found in litters about two weeks old appear *fully as mature* as do the other members of the litter, but they are much less active. In litters like those described above the smaller individuals are always *less mature* than the other rats, although equally as vigorous and well nourished.

In cases of this kind all members of the litter must have developed from ova belonging to the same period of ovulation, since it is very improbable that a second period of ovulation ever follows immediately after the first. There are two possible explanations for these cases. If at some period of ovulation one or more of the ova were unusually slow in maturing they might not be liberated until two or three days after the rupture of the more mature follicles, and so would not be fertilized at the first mating. Such ova might, however, be fertilized at a subsequent mating; for the period of heat in the rat extends over several days and copulations take place frequently during this time, as the investigations of Miller have shown. As the minimum gestation period in the albino rat is 21 days, ova that were fertilized late could not reach the proper stage of maturity to be born with the embryos that developed from the first ova fertilized, and consequently there would be a considerable interval between the births of different members of the litter. According to this explanation such litters are good examples of superfecundation.

There is another possible explanation for these cases, namely, that all of the individuals in the litter were developed from ova that were fertilized at the same mating, but that for some reason, possibly on account of faulty implantation, some of the embryos received less nourishment than the rest and so reached maturity later. Such conditions, it seems to me, would tend to produce runts, and not merely to retard normal development.

On dissecting pregnant females one frequently finds one or more embryos that are much smaller than the rest. While in some instances such small embryos appear normal and are presumably

either runts or embryos that have resulted from superfecundation, in the majority of cases they are pathological, probably because of faulty implantation of the ova. If such pathological embryos are ever born with the rest of the embryos they are destroyed at once by the mother, as they are never found among the normal newborn young.

3. CASES OF SUPERFŒTATION.

It has been maintained by many physicians that ovulation does not occur during pregnancy and therefore that the conception of a second foetus by a pregnant woman is impossible. Cases seemingly those of superfœtation have been ascribed to the presence of a bifid uterus, or they have been assumed to be the result of a twin pregnancy in which one foetus was blighted. Undoubtedly many so-called cases of superfœtation can properly be attributed to one or to the other of these causes, but there are a number of well-authenticated cases, such as those cited by Bonnar ('65), which seem explicable only on the assumption that superfœtation can occur in woman under exceptional conditions.

In the lower mammals superfœtation is seemingly of rare occurrence. An examination of the evidence shows that many cases that have been reported as due to superfœtation are unquestionably instances of superfecundation or of blighted ova. A very probable case of superfœtation in sheep was reported by Arrowsmith in 1834, while the observations of Christopher ('86) show that in the cat ovulation can occur during pregnancy and, therefore, that superfœtation in this species is possible, although it is not known to have taken place.

In the course of my investigations on the rat I have found two cases which are seemingly due to superfœtation. Female 44₂₉ had a litter of four young born on December 20, 1910. The male was removed when the litter was discovered and the nest was left undisturbed for fourteen days, when the litter was examined for the sex ratio. At this time the four rats born on December 20 were well developed, and they weighed from 15.5 gm. to 16.4 gm. each. In addition to these rats the nest was found to contain seven very small rats that had apparently been born only a

short time before as they were bright red in color and weighed less than 5 gm. each. Between the birth of the first four members of the litter and of the last seven there was an interval of about fourteen days.

Female 6A₆₃² gave birth to her first litter of three young on February 26, 1912. Thirteen days later the nest was examined and found to contain seven newborn rats that weighed from 4 gm. to 4.5 gm. each. The older members of the litter weighed at this time 10.1 gm., 10.2 gm. and 10.5 gm. respectively. The interval between the birth of the first and of the last members of the litter was in this instance about twelve days. In each of these cases the female with her young occupied an entire cage, so there was no possibility that the newborn rats could have belonged to another female. None of the small rats in these litters were runts, and, with the exception of one that was killed for a museum specimen, all of them were raised to maturity and some were used for breeding purposes.

Female 4A₂₉ was not examined after her death for any possible malformation of the genital organs. A careful autopsy was made of female 6A₆₃², however, and there was no evidence whatever of any abnormality either in the ovaries or in the uterus. This rat had three other litters besides the one described above, and in each of these litters all of the individuals were born during the one period of parturition.

The cases of superfecundation described in the second section of this paper indicate that a single period of ovulation may extend over three or four days, but it is difficult to see how embryos, born at intervals of two weeks, could possibly have developed from ova belonging to the same period of ovulation. To assume that some of the ova liberated at a given period of ovulation were fertilized at once while others remained in the tubes or in the uterus for nearly two weeks before they were fertilized seems unwarranted; for while it is not known how long mature ova can live without fertilization, it is improbable that they can live for more than a few days at most. That part of the ova belonging to a certain period of ovulation should produce embryos that would be born after a normal gestation period of about 21 days while the rest of the ova had their development so delayed that

they were born only after a gestation period of about 35 days also seems highly improbable. The most plausible explanation for these cases seems to me to assume that the two ovaries acted independently, ovulation occurring in one ovary some little time before it took place in the other. If copulation followed each ovulation two sets of embryos would develop in the uterus simultaneously, and they would be born at different times, depending on the interval between the two periods of ovulation.

Conditions which retard ovulation from one ovary for a greater or a less period of time and so make superfœtation possible must occur very rarely in the rat, since the two cases described are the only ones that have been found in the course of my experiments.

SUMMARY.

1. The normal period of gestation in non-lactating albino rats ranges from 21 to 23 days.

2. The gestation period in lactating albino rats is of normal length if the female is suckling five or less young and is carrying five or less young.

3. The gestation period may be prolonged from one to six days if an albino female, suckling five or less young, is carrying six or more young.

4. The period of gestation is always prolonged when a female is suckling six or more young. In these cases the number of young in the second litter seems to have less influence on the length of the gestation period than has the number of young suckled; but if both litters are very large the gestation period may be extended to 34 days.

5. In the albino rat ovulation takes place within a few hours after parturition.

6. Lactation does not delay ovulation, but the suckling of a litter that contains six or more young seems to lessen the food supply to the foetal young and so retards their development.

7. Superfecundation occurs occasionally in the albino rat and causes an interval of two or three days between the birth of different members of the litter.

8. In rare instances ovulation takes place in the albino rat during pregnancy and superfœtation occurs. In two cases of

this kind litters have been produced at intervals of about two weeks.

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